ABSTRACT: Feed efficiency is a very important trait in poultry and has been a breeding objective for over 50 years. Phenotypic measures are required on an individual basis to drive improvements in feed efficiency, while this has traditionally been achieved via individual caged birds, it is giving way to RFID based measurements. Improvements in feed efficiency have been achieved because of the high fecundity, intense selection pressure and short generation intervals. Reproductive capacity has helped achieve these gains but also the unique anatomy, physiology and behaviour has allowed poultry to be efficiently farmed. Reproductive and cull traits like pendulous crop are negatively correlated with improved feed efficiency and must also be considered. This paper will reflect on the methods used for the improvement of feed efficiency in the past but also considers strategies currently being used and those that may be important in the future.

Keywords: poultry; genetics; feed efficiency; selection; residual feed intake

Introduction

Genetic selection for improved feed efficiency is naturally important in all farmed livestock species but in poultry the results of that selection can be easily seen due to their short generation interval and the high selection pressure. There are a number of poultry species, of which chickens, turkeys, ducks and quail would be most economically significant of those farmed. Within this, the vast majority are chickens for both meat (broilers) and egg production (layers) but the other species certainly make contributions. In all these industries, feed averages between 60-70% of the cost of production, consequently, the importance of feed efficiency in the breeding goal is large.

The uniqueness of the poultry species in their anatomy, physiology, behavior and also the farming methods make them a challenge to breed and it can also place some limitations. In terms of the gastrointestinal tract (GIT) and physiology they are monogastrics with the largest differences being, the absence of teeth for mechanical breakdown of food, the presence of a crop, the muscular gizzard, relatively short intestines and paired caeca. Added to this are the methods of farming and raising birds in large flocks (5-20,000 birds), making feeding behavior, aggression and mortality all factors that can have a significant effect on the calculated flock feed efficiency. Consequently, other traits can have as large an effect on improvements in feed efficiency as direct selection on a feed efficiency trait itself, be it FCR, RFI or some other defined efficiency trait. What this results in is that feed efficiency should be also be considered within the context of the whole breeding objective and other traits that may affect total flock feed efficiency.

For genetic improvement, the measurement of individual or family information is difficult and expensive as it often requires individual or sibling cages and the measurement of feed over a period of time. Increasingly across all the species there has been a movement to group housing using RFID technology. Rapid improvements in both hardware and software have made the implementation relatively simple given the investment. Lastly, a decision must be made on investments in a breeding program and the increasing use of genomic information also comes with a significant cost.

The Unique Anatomy of the Avian Gastrointestinal Tract

The avian gastrointestinal tract is simple and very efficient. This should be viewed from an evolutionary context of the necessity of a bird to fly or escape from predators. The biggest difference compared to other monogastrics is the absence of teeth for food breakdown, the presence of a crop for food storage, the muscular gizzard and paired functional caeca. The small and large intestines are relatively similar to other monogastrics. The simplicity and compactness of the system means that birds require relatively high quality and easily digested feed as they do not have the ability to metabolise foods like the ruminants or the hind gut fermenters, although some fermentation does occur in the caeca.

The crop is a large dilation of the oesophagus and has a distinct evolutionary function so that birds can eat rapidly and leave to later digest the food in relative safety. For domesticated poultry, a crop would appear to be less important as they are fed ad libitum and are free from predators. As we show later the presence of the crop does have some consequence in the selection for feed efficiency. The proventriculus produces enzymes and hydrochloric acid for the chemical breakdown of food and these secretions and food then move into the gizzard for physical breakdown that is required due to the lack of teeth. The insides are highly keratinised and often will contain grit or stones if supplied to aid in the breakdown.

The small intestine is relatively short and is the site of most of the digestion and nutrient absorption. Small intestinal villi length and total surface area affect nutrient absorption and any diseases that can blunt these villi such as coccidiosis and various enteric viral infections such haemorrhagic enteritis can decrease surface area and consequently decrease the efficiency. It has been shown that selection for feed efficiency can also alter the weight
gastrointestinal tract as a correlated response (de Verdal, et al., 2013) and it may be that functionality of the GIT becomes a limiting factor for further improvement in FCR. Food passes through the small intestine in around three hours and there is about 1 hour for absorption in the duodenum and jejunum and it may come to the point that feed, even when highly digestible, cannot be absorbed at a fast enough rate. This leads to the apparent metabolisable (AME) energy decreasing as it cannot be absorbed rapidly enough.

The exact role of the caeca in the nutrition of highly efficient poultry is uncertain but it does play a role in recycling nitrogen from urine, fermentation of non-absorbed nutrients and absorbing salts and water (Svihus, et al., 2013). Lastly, the large intestine is relatively short and serves a similar purpose as other species to regulate water and salts comparable to the large intestine.

**Advances in feed efficiency – layers, broiler chickens & turkeys**

For simplicity, broilers and turkeys are grouped together due to their similarity of selection objective. The major components of the selection objectives have been invariably faster growth or greater body weight, feed efficiency and increased yield (mostly as breast meat). Heritabilities for feed efficiency traits are all in the moderate range (0.11-0.41) (Willems, et al., 2013). Improvements to the same weight (i.e. 2.5kg) over the past 35 years for broilers have seen improvements in FCR from 2.40 to 1.80 based on primary breeder production guides. For a 1.8kg broiler, FCR was compared between a RBC line from 1957 (4.42) and a 2001 strain (1.47), representing an improvement of 2.95 (Havenstein, et al., 2003). In turkeys, similarly large improvements have been made but comparisons are less easily estimated as to a set weight in broilers, the turkey industry slaughter weights have continued to increase. Similarly using primary breeder goals, a turkey tom in 1985 at 24 weeks would weigh 17.5kg with an expected FCR of 3.25 compared to a modern day strain could be assumed to reach the same weight in 17 weeks and have a feed conversion of 2.35. In a similar study to the broilers above, comparing older breeds it was estimated that selection programs alongside management techniques had improved FCR in the turkey by approximately 20% (Havenstein, et al., 2007).

Similar heritability values for the efficiency of egg production can be found in laying hens to those found in broilers and turkeys (Wolc, et al., 2013). The improvements in feed efficiency can be easily seen in the layer house performance results from the North Carolina layer test that has operated for over 50 years. Improvements in layer house performance from 1958 to 2011 saw an improvement in egg production FCR from 3.07 to 2.03 and from 2.90 to 2.00 in brown and white strains, respectively.

In all these groups, improvements of approximately 2% per year have been the norm for this entire period. In unpublished work in turkeys we have monitored the changing levels of genetic variance from long-term selection and have shown no decrease, consequently, we can assume that the rate of genetic progress will not be limited in the near future. The primary breeders in both the layer and broiler industries also continue to achieve similar improvements so we could assume the same is also true for those programs although intense selection on efficiency has occurred for a longer period.

**Methods for the measurement of feed efficiency in poultry**

The selection for efficient poultry has been achieved through phenotyping large numbers of individuals. Until recently, this was achieved through simple individual cage measurements where the production (i.e. weight gain or egg production) over a given period and the feed intake was measured. This has been used for well over 40 years. While highly successful there has been a movement to other measures because individual cages are labour intensive, expensive to operate and there could be welfare concerns (Willems, et al., 2013).

With significant improvements in computing power and software, the development of an RFID tagged technology to measure feed intake in large groups is now used widely across the sector (Howie, et al., 2010). The advantages include phenotyping larger numbers within the same space, the environment more closely resembles real life conditions where the genotypes are expected to perform, and lastly, it allows normal social behavioural traits to be expressed. Table 1 shows the relationship between some simple measures of feeding behaviour and their relationship to two feed efficiency traits. It shows that turkeys that eat fewer but larger meals are also the most feed efficient. The large amounts of information that can be collected on meals and behaviour has yet to be fully explored and if this information adds more to the selection for feed efficiency that just using simply the feed intake. Alternatively, this additional information may be used to either monitor or change feeding behaviour as this may be correlated with other unwanted behaviours such as aggression and pecking.

Another measure of feed intake and efficiency that has been considered was the use of infrared measures of eye and skin temperature at different points on the bird (Case, et al., 2012). Infrared showed strong correlations with feed intake but unfortunately, when corrected for when using RFI, there was no relationship to efficiency. Although, as will be discussed later, where feed intake level should be monitored, such as in layers, this method of phenotyping may be useful.
pendulous crops could be a behaviourally related problem could easily be surmised that the relationship with the relationship between meal size and feed efficiency it al., 2013). Other factors such as the availability of foraging social facilitation may play contributing roles (Dalton, et al., 2013). However, it has been suggested that the environment, development of the behaviour, early lighting regimes and social facilitation may play contributing roles (Dalton, et al., 2013). Other factors such as the availability of foraging material, lighting, diet composition, stocking densities, and group dynamics may also affect levels of pecking. The link between selection for feed efficiency and behavioural change has been anecdotally suspected as there are differences in behaviour between strains and there is some evidence for changes in behaviour as a correlated response to selection for feed efficiency (Pelhaitre, et al., 2012). Direct selection for behavioural response in layer chickens using social effects model have shown promise but with the effect on FCR through decreases in mortality as discussed later and not related directly to selection feed efficiency or a correlated behavioural trait (Ellen, et al., 2010).

### Feed components and possible genotype x environment interactions

The simplicity and compactness of the avian digestive system means that birds require relatively high quality and easily digested feed as they do not have the ability or time to metabolise foods like other species. Consequently, there have been a number of strategies to increase the digestibility of such as the addition of enzymes and different milling techniques. The question that needs to answer is what diet is the best to use for phenotyping purposes. There are many different diets but by far the simplest distinction can be made, is it corn or wheat based? This simple distinction on components can also be made on world poultry production, with corn-soybean dominating in North and South America and wheat based more commonly but not always used in Europe. The distinction between diet components is very important as there are differences in the genetic parameters for the digestibility corn and wheat based diets (Mignon-Grasteau, et al., 2010).

The consolidation of the primary breeding companies across all of the product groups has led to a small number of breeders supplying a very large section of the available market (Wood, et al., 2006). The advantages and disadvantages of this situation will be discussed but the one of the main responsibilities of the breeding company is to supply a genetic package that performs under the given conditions. In order to take genotype by environment interactions into account, primary breeders can follow different strategies, the first of these is to establish pure line breeding farms in various (geographic) regions and thus develop specialized products locally. The second is to use recurrent testing; testing of (pedigreed) crossbred products on different commercial farms and include this information in the breeding value estimation for pure lines. Thirdly, testing pure lines simultaneously on pedigree farms and commercial farms and determining the ranking of pure line birds based on both types of information.

With differences in the feed components a breeding company must produce a genetic package that performs under the given environmental conditions. Currently we are defining the environment as feed but this could also be other environmental factors such as temperature (particularly heat), management and pathogen exposure. For all species decentralized breeding units are an expensive method to operate a breeding program but with the consolidation of breeding companies there are examples of nucleuses running simultaneously on several continents.
in layers, broilers and turkeys. Recurrent testing is widely used by the layer breeding industry as a method to sample different environments for a breeding program to attempt to eliminate this GxE effect or at least be able to account for it (Albers, et al., 2002).

The major difference in these two diets results in a larger non-starch polysaccharide (NSP) component within the wheat based diet. Increasing the proportion of NSP decreases digestibility and you also get an increase in water intake (Patterson, et al., 1989). The high molecular weight polysaccharides increase the viscosity of the food passing through and as a result birds consume approximately 50% more water. In the same lines that showed differences in the genetic parameters for the digestibility of corn and wheat based diets, it was also shown that there was genetic correlation with water intake and excretion (de Verdal, et al., 2011). It could be suggested that a selection program undertaken using wheat based diets could also be inadvertently selecting for a higher water intake genotype. These birds could perform better on that diet with a greater amount of water present to decrease viscosity and transport through the GIT. There are certainly differences between genotypes for water intake within and across the genetic lines used by the primary breeding companies.

The differences in water intake between genotypes has significant welfare implications as barn conditions become more difficult to manage resulting in skin and footpad lesions (Allain, et al., 2013). The use of foot-pad lesions in the processing plant as a proxy for management is being considered as a method to grade producers and determine allowable stocking densities.

**Other effects on feed efficiency – mortality/livability**

As stated in the introduction, the measurement of poultry feed efficiency can be greatly influenced by other traits and of particularly importance is survival to slaughter. Late mortality, meaning birds that die close to slaughter age is both an economic and animal welfare issue. As an example, if we assume an average turkey flock slaughter weight of 20kg and a flock FCR of 2.40 as a starting point a 0.05% increase in mortality in the last week can have an effect on flock FCR of 0.03. A similar calculation can be made for broilers and assuming a 2.7kg slaughter weight and 1.71 FCR with a 0.05% increase in late mortality can yield up to an increase of 0.11 in the flock FCR. There are a number of assumptions that the increase in mortality occurs in the last few days, such as a size scaling effect between broiler chickens and broilers. However, the take home message is that small changes in survival to slaughter can make large measureable differences to a producer.

**Genomic selection**

All of the species are evaluating genomic selection as a tool to increase the accuracy of selection for the entire breeding objective of which feed efficiency is only one component. The greatest progress is likely to be made in layers with reductions in generation interval by earlier selection of sires without the need for progeny test information (Sitzenstock, et al., 2013). This is shown by all the major layer breeding companies making substantial investments in genomic breeding. For the meat species the advantages are not of the same magnitude as it relies solely on improvements in breeding value accuracy without a change in generation interval, never the less, substantial investments have been made in genomic breeding in these programs too.

Lastly, the symbiotic microbial population within the GI tract is being more closely studied. This has been due the advances in next generation sequencing technology. The microbiome profile has the potential to affect traits such as feed efficiency and in practice the use of antibiotics, anticoccidials and growth promoters have been used to increase growth and improve feed efficiency by changing these profiles. By examining the changes in the microbiome resulting from these modulators it may be possible to select for an advantageous profile or metagenome (Danzeisen, et al., 2011). The microbes within an animal rely upon it for their environment; consequently, this could be considered the phenotype of the animal on which to select to decrease the use of the above mentioned feed additives.

**Conclusion**

Selection for feed efficiency continues to be major goal in poultry breeding programs, the success of which can be seen in the continued reduction in feed inputs into each of the systems. Identifying diets and breeding to reduce GxE interactions continues to be a challenge and there could be good arguments to work more closely with ingredient manufacturers in the future. Challenges will undoubtedly be reaching a biological maximum but at this stage this is not in the foreseeable future. Including negatively correlated traits in an index remains important but the challenge will be to also include relevant behavioural traits.

**Literature Cited**


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